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# JOURNAL OF THE ARNOLD ARBORETUM

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VOL. 56

APRIL 1975

NUMBER 2

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## REPRODUCTIVE ADAPTATIONS IN PROSOPIS (LEGUMINOSAE, MIMOSOIDEAE)<sup>1</sup>

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THE GENUS *Prosopis* L. comprises about 40 species of shrubs and trees, which are distributed over the drier, warmer areas of the Americas, Africa, and western Asia (Burkart, 1940; Johnston, 1962). In this paper we will present quantitative data concerning the phenology, the production of flowers, fruits, and seeds, the destruction of seeds by bruchid beetles, and the percentage of seed germination in three related arborescent species of *Prosopis*. On the basis of this data, together with some additional qualitative observations, we will discuss some aspects of the adaptive "strategy" of reproduction in these species, a "strategy" that is probably shared by other arborescent phreatophytes of semidesert regions, particularly those belonging to the Mimosoideae. This study is part of a comprehensive investigation of convergent adaptation in desert regions with similar climates (Solbrig, 1972a).

### MATERIALS AND METHODS

Although some data will be presented for other species, we are primarily concerned with the South American species *Prosopis chilensis* (Mol.) Stuntz and *P. flexuosa* DC. and the North American species *P. velutina* Wooton.<sup>2</sup> More precisely, *P. chilensis* occurs in southern Peru, central Chile, and west-central Argentina (Burkart, 1940); *P. flexuosa* is endemic to west-central Argentina (Burkart, 1952); *P. velutina* occurs in Arizona and the Mexican state of Sonora (Benson, 1941; Johnston, 1962). All three species are trees of medium height (rarely exceeding 18 meters) which, owing to their extremely deep root systems, are able to survive as phreatophytes in semiarid shrublands where few other trees can grow. Although there are no precise studies of the underground water resources at the particular study sites of this investigation, anecdotal information from wells in the areas where the three species occur indicates

<sup>1</sup> Contribution of the Structure of Ecosystems Program of the US/IBP.

<sup>2</sup> Nomenclature follows Burkart (1952) for South American species and Johnston (1962) for North American species.

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that at depths of from 30 to 100 meters there are permanent sources of water. Observations by Vervoorst (1954) indicate that roots of *P. flexuosa* may reach 80 meters in depth, making the tree capable of tapping a deep supply of water that is unavailable to most other plants. We feel it to be a reasonable assumption that the other two related species, of similar height and occurring under much the same environmental conditions, have the same mode of survival.

The bulk of the observations were made in two areas. In South America the study sites were located in the Bolsón de Pipanaco, near the town of Andalgalá, Catamarca Province, Argentina. The Bolsón is a basin of about 3000 square miles, nearly surrounded by mountains, with an annual rainfall ranging from 75 mm. at the southern end to 300 mm. at the northern end. Nearly all of the rain comes during the summer months, December through March (FIGURE 1). In North America our observations were made in the area surrounding Tucson, Arizona, principally on the Silver Bell Bajada. The climate here (FIGURE 2) is generally similar to that of the Argentine study site, with a comparable total annual rainfall; one notable difference, however, is that in Arizona the rain is divided between two rainy seasons, one in the winter and one in the summer. The vegetation of the two areas is similar in structure and biomass, but not in floristic composition. There are, however, several dominant genera (*Prosopis*, *Larrea*, *Acacia*, *Cercidium*) that are represented in the two areas by the same or closely related species (Solbrig, 1972a, b).

**Phenology.** Over a two-year period, an investigation was conducted on the phenology of *Prosopis chilensis* and *P. velutina*.<sup>3</sup> Six populations of the former and three of the latter were studied, with ten trees in each population randomly selected and marked for observation. At regular intervals (weekly for some sites, monthly for others) the populations were visited, and the stages of flowering, fruiting, leaf-production, and leaf-fall were observed. The stages were recorded as positive or negative; no attempt was made to quantify the intensity of the stage. Thus quantitative estimates can be made regarding, for instance, the proportion of the population that had at least one fresh flower bud or one incipient fruit at a given time, but no such estimate can be made of the proportion of plants that had numerous fresh buds. We have, however, complemented the quantitative data with qualitative observations on the relative intensity of flower and fruit production through time.

**Flower and fruit production.** An investigation of flower and fruit production was carried out with two objectives: the determination of the relationship between the number of flowers produced and the number of mature fruits, and the estimation of the annual seed yield of an average tree. In order to obtain the necessary data, we adopted the following pro-

<sup>3</sup> The observations in Argentina were made by J. LeClaire, P. Reppun, G. Brown, and P. Cantino; the Arizona observations by T. W. Yang and Y. Abe.



cedure. Ten trees of each of the three species were chosen at random, with no more than five trees in the same population. (Five populations of *Prosopis flexuosa* were sampled, seven of *P. chilensis*, and two of *P. velutina*.) On each tree one or two large branches were chosen for accurate flower-counts; the choice of branches was not random in that only branches within reach of the ground were considered, but within the subset of conveniently located branches the choice was made randomly. On each branch an accurate count was made of the number of inflorescences and the lengths of 25 of them, the number of incipient fruits produced, and the number of mature fruits. The counts and measurements were done without removal of inflorescences or fruits. From other branches on the same trees inflorescences were removed, their lengths measured, and the number of flowers counted, from which data a calculation was made of the average number of flowers per centimeter of inflorescence. By multiplying the average number of flowers per cm. times the average inflorescence length (calculated from the 25 inflorescences measured on the marked branch) times the number of inflorescences on the branch, we arrived at an estimate of the number of flowers on the branch. Using this estimate and the counts of incipient and mature fruits on the branch, we calculated the number of fruits initiated and fully developed per thousand flowers.

**Seed destruction by bruchid beetles.** Using the same ten trees of each species chosen for the study of flower and fruit production, we conducted an investigation to determine the extent of seed destruction by developing bruchid beetles, the timing of the damage, and the variation in the amount of damage from tree to tree. In the case of *Prosopis chilensis*, eight of the trees were located in a district that was heavily grazed by herds of domesticated goats. After only a few weeks the goats had removed all the fruits from the ground, necessitating the selection of four new trees in another area to continue the study. Unfortunately there was a time lapse of several weeks between the last sampling of the original trees and the first sampling of the newly chosen trees.

In Argentina a weekly sample of ten fruits was taken from each tree and a second sample of ten fruits from the ground beneath the tree. The sampling was initiated when the fruits appeared nearly ripe and was continued for three and one-half months. Each of the collected fruits was inspected and the number of seeds with and without bruchid emergence holes was recorded. The weekly samples of eight of the trees (four of *Prosopis flexuosa* and four of *P. chilensis*) were sent to Ing. Agr. Arturo Terán, who recorded further bruchid emergence in the succeeding weeks and identified the bruchids. In Arizona fruit samples from *P. velutina* were collected only once, at maturity. The bruchids that emerged were sent to Dr. John Kingsolver for identification.

In an additional study of seed damage by bruchids, samples of mature fruits were collected over a three-year period from 290 *Prosopis* trees and shrubs, representing 83 populations and 15 species, in Argentina, Mexico,



and the United States. Up to 10 fruits from each tree were shelled, the tough endocarps broken, and the number of fully developed, underdeveloped, and bruchid-damaged seeds recorded. In all, close to 30,000 seeds from about 2600 fruits were inspected. Because of the time-consuming nature of the seed-inspection process, it extended over a six-month period after collection of the fruits, allowing for some secondary infection of the fruits resulting from oviposition by emerging adult bruchids. As a result, the data may indicate a greater amount of seed damage, in some cases, than actually existed at fruit maturity. Nevertheless, the data serve to give a rough idea of the amount of damage that occurs in different populations and species of *Prosopis*.

**Germination and seedling development.** Many of the seeds collected in the previous study were germinated for subsequent use in genetic studies using isozymes (Solbrig & Bawa, in preparation). The seeds were removed from the endocarps, scarified, and planted in a sandy-loam mixture in plastic trays. The trays were placed in an incubator with artificial light, watered copiously, and maintained at a constant temperature of 68° F. After approximately six weeks, the seedlings were transplanted into three-inch pots and kept in a greenhouse; after a year, they were transplanted into six-inch pots. Measurements of the seedlings were made at regular intervals.

An additional experiment was conducted with the seeds of *Prosopis chilensis* to investigate the effect on the germination rate of previous passage through the intestinal tract of livestock. In two trials, seeds were removed from the excrement of goats and horses and planted in trays of soil collected at the edge of a wash where *P. chilensis* occurs naturally. The soil was strained before use to remove any seeds already present. Two other sets of seeds were planted as a control, one consisting of seeds removed by hand from their endocarps without intentional scarification of the seed coat and the other consisting of seeds with endocarps intact. The soil was kept moist for a two-week period, after which time the number of seedlings in each category was recorded. No attempt was made to maintain a constant temperature during the experiment; the trays were kept side by side on a window sill, where they received full sunlight during part of the day. Room temperature ranged from a minimum of 69° to a maximum of 97° F.

## RESULTS

**Phenology.** The timing of leaf production in *Prosopis chilensis*, which has a winter-deciduous habit in the region of our study, was highly regular, varying little from site to site or between the two years of the study. Leaf initiation commenced in September, well before the onset of the summer rains, proceeded at a high rate for about two months, and then continued at a much reduced and rather irregular pace throughout the summer. In April and May the production of new foliage ceased and



leaf-fall began, leading once again to the nearly bare trees of midwinter (FIGURE 1).

Flowering of *Prosopis chilensis* occurred in a single burst of bloom in October and November. The timing varied by as much as two weeks from site to site, but within any given population the onset of flowering was highly synchronized. The regularity of the event, coupled with the fact that it occurred before the end of the winter drought, leads us to believe that flowering must be triggered by an environmental factor other than water supply, most likely photoperiod. The fruits reached maturity in mid-to-late December and dropped soon afterwards, the vast majority falling to the ground by the end of January (FIGURE 1).

Although we have no quantitative data on the phenology of *Prosopis flexuosa*, we observed that the entire pattern of foliage, flower, and fruit production was very similar to that of *P. chilensis*.

The Arizona data, generously given to us by T. W. Yang, plus previous work on the phenology of *Prosopis velutina* (Glendening & Paulsen, 1955; Turner, 1963), indicate a pattern of phenology for that species (FIGURE 2) that is basically similar to that of *P. chilensis*, but the data and resulting charts are a bit difficult to interpret for two reasons. First of all, the timing of the rainfall in 1972 at the Arizona site (FIGURE 2) was highly unusual. February and March, months during which rains can be expected in that region, were exceptionally dry, whereas October and November, normally dry months, experienced heavy rains. The timing of the rainfall in 1973 was more typical of the region. Secondly, data collection began in June, 1972, after that season's leaf production and blooming were already in progress.

In 1973, leaf initiation in *Prosopis velutina* began in March, proceeded at a high rate on all trees until mid-May, and declined to zero by the end of July. In 1972, leaf initiation may also have begun in March, but there were additional periods of peak leaf production in July and August, and again in October, the latter presumably in response to the exceptional October rainfall.

The initiation of blooming in *Prosopis velutina*, as in *P. chilensis*, is synchronized within populations and very likely under photoperiodic control. In 1972, blooming probably began at the Arizona site in May, as it did in 1973; we lack data earlier than June, 1972, but the production of fruits in June and July of 1972 is proof that blooming must have occurred before the study was initiated. The fact that only 40 per cent of the trees produced fruits during that period is evidence that this was a poorer bloom than that of May, 1973, probably because of the scarcity of rainfall in February and March of 1972. Additional periods of bloom occurred in July and in late August, 1972, in response to summer rainfall. In the more "normal" year, 1973, on the other hand, there was a single period of bloom, peaking in May and June.

In summary, it appears that blooming in both *Prosopis chilensis* and *P. velutina*, and perhaps leaf production as well, are initially triggered by an environmental stimulus other than water availability, probably photo-



## CHILENSIS

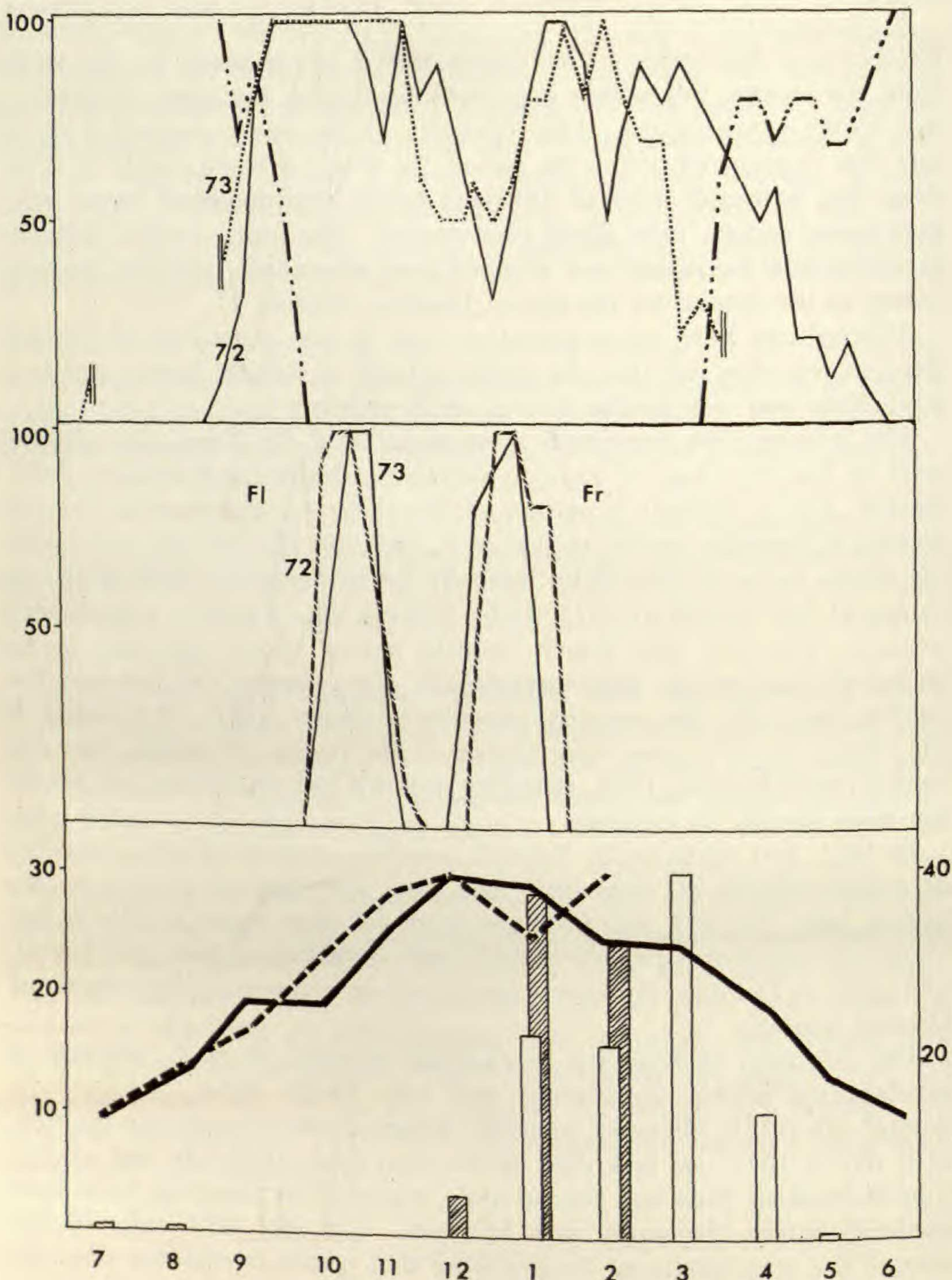


FIGURE 1. Phenology of *Prosopis chilensis* in Andalgalá. UPPER GRAPH: leaf growth and leaf fall as a percentage of plants in the population (solid line, leaf growth in 1972-73; dotted line, leaf growth in 1973-74; dashed dots, leaf fall in 1973). MIDDLE GRAPH: flowering and fruiting as a percentage of plants in the population (solid line, 1972-73; broken line, 1973-74). LOWER GRAPH: temperature in degrees centigrade (solid line, 1972-73; broken line, 1973-74) and rainfall (white bars, 1972-73; dashed bars, 1973-74). Abscissa represents months of the year; ordinate represents percentage (upper two graphs) or degrees (lower graph, left) and millimeters (lower graph, right).



VELUTINA

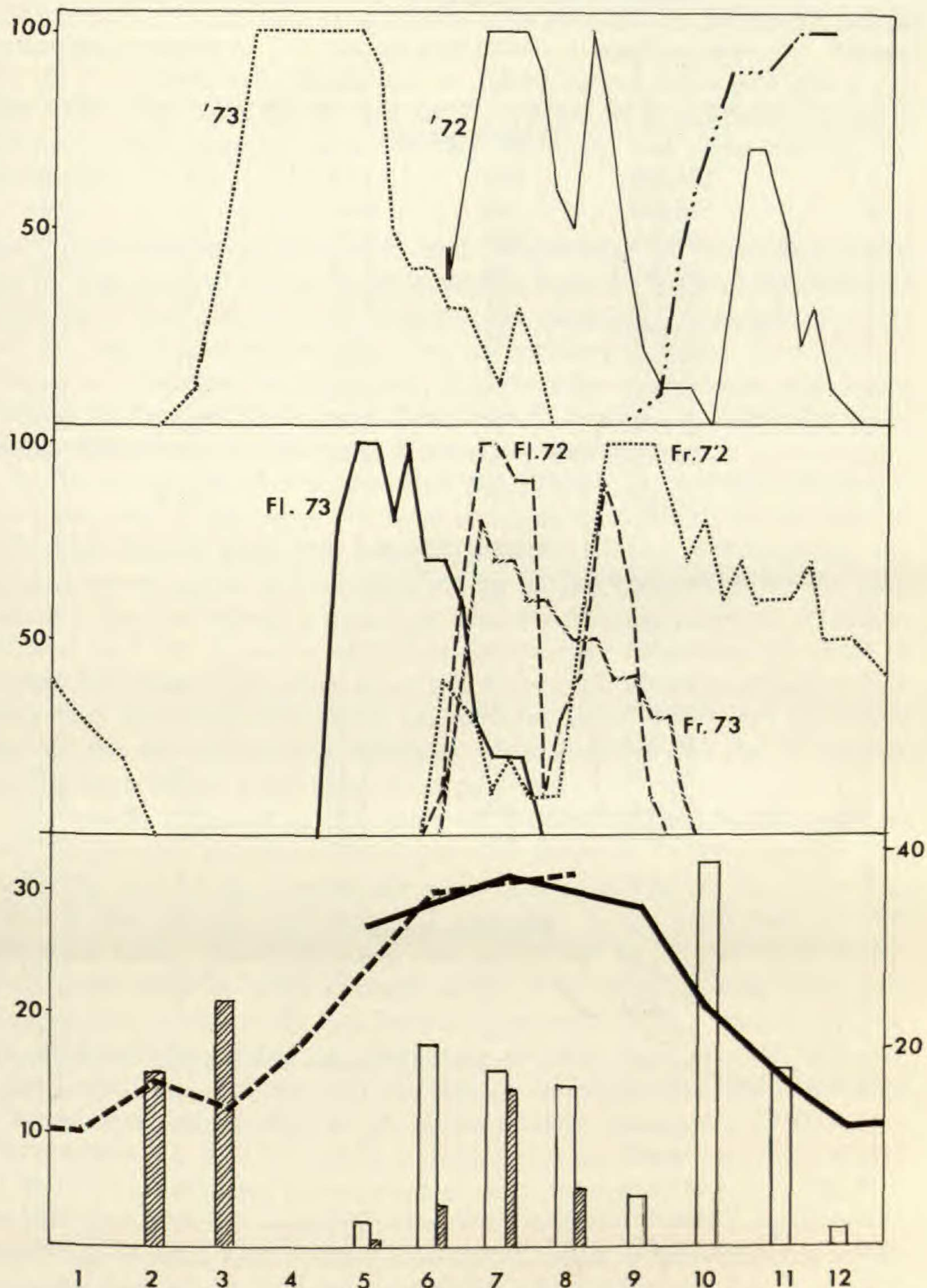


FIGURE 2. Phenology of *Prosopis velutina* in the Tucson area. UPPER GRAPH: leaf growth and leaf fall as a percentage of plants in the population (solid line, leaf growth in 1972; dotted line, leaf growth in 1973; dashed dots, leaf fall in 1972). MIDDLE GRAPH: flowering and fruiting as a percentage of plants in the population (dashed line, flowering in 1972; solid line, flowering in 1973; dotted line, fruiting in 1972; broken line, fruiting in 1973). LOWER GRAPH: temperature in degrees centigrade (solid line, 1972; dashed line, 1973) and rainfall in millimeters (white bars, 1972; hatched bars, 1973). Abscissa represents months of the year; ordinate represents percentage (upper two graphs) or degrees (lower graph, left) and millimeters (lower graph, right).



TABLE 1. Number of flowers, incipient fruits, and mature fruits.

| TREE NO.                  | NO. FLOWERS | INCIPIENT FRUITS |      | MATURE FRUITS |      |
|---------------------------|-------------|------------------|------|---------------|------|
|                           |             | No.              | %    | No.           | %    |
| <b>Prosopis flexuosa</b>  |             |                  |      |               |      |
| 1                         | 184,000     | 689              | 3.74 | 222           | 1.21 |
| 2                         | 76,000      | 50               | 0.66 | 25            | 0.33 |
| 3                         | 86,000      | 427              | 4.97 | 56            | 0.65 |
| 4                         | 38,000      | 40               | 1.05 | 1             | 0.03 |
| 5                         | 18,000      | 21               | 1.17 | 0             | —    |
| 6                         | 20,000      | 55               | 2.75 | 25            | 1.25 |
| 7                         | 45,000      | 2                | 0.09 | 0             | —    |
| 8                         | 28,000      | 75               | 2.68 | 32            | 1.14 |
| 9                         | 37,000      | 51               | 1.38 | 28            | 0.76 |
| 10                        | 28,000      | 40               | 1.43 | 15            | 0.54 |
| $\bar{x}$                 | 56,000      | 145              | 2.59 | 40.4          | 0.72 |
| <b>Prosopis chilensis</b> |             |                  |      |               |      |
| 1                         | 45,000      | 92               | 2.04 | 3             | 0.07 |
| 2                         | 47,000      | 13               | 0.28 | 0             | —    |
| 3                         | 43,000      | 148              | 3.44 | 0             | —    |
| 4                         | 28,000      | 31               | 1.11 | 1             | 0.04 |
| 5                         | 20,000      | 14               | 0.70 | 0             | —    |
| 6                         | 16,000      | 15               | 0.94 | 2             | 0.13 |
| 7                         | 40,000      | 73               | 1.83 | 4             | 0.10 |
| 9                         | 60,000      | 100              | 1.67 | 11            | 0.18 |
| 10                        | 115,000     | 145              | 1.26 | 15            | 0.13 |
| $\bar{x}$                 | 46,000      | 70.1             | 1.52 | 4             | 0.09 |
| <b>Prosopis velutina</b>  |             |                  |      |               |      |
| 1                         | 263,905     | —                | —    | 116           | 0.44 |
| 2                         | 89,300      | —                | —    | 52            | 0.58 |
| 3                         | 19,975      | —                | —    | 7             | 0.35 |
| 4                         | 62,980      | —                | —    | 130           | 2.06 |
| 5                         | 119,850     | —                | —    | 211           | 1.76 |
| 6                         | 90,005      | —                | —    | 13            | 0.14 |
| 7                         | 18,095      | —                | —    | 6             | 0.33 |
| 8                         | 39,245      | —                | —    | 98            | 2.50 |
| 9                         | 287,405     | —                | —    | 89            | 0.31 |
| 10                        | 123,845     | —                | —    | 9             | 0.07 |
| $\bar{x}$                 | 111,461     | —                | —    | 73            | 0.65 |

period; but the existence of later blooms and the continuation of leaf production are dependent on sufficient rainfall.

**Flower and fruit production.** Each of the three species studied produced an average of between 220 and 240 flowers per inflorescence, of which



usually no more than two developed into mature fruits; many inflorescences produced no fruit at all. In *Prosopis flexuosa* only 26 flowers in 10,000 initiated development into fruits, and about 7 reached maturity (TABLE 1). In *P. chilensis* only about one in 10,000 flowers developed into a mature fruit. The fruit/flower ratio of *P. velutina* was similar to that of *P. flexuosa*. The possible causes of this extremely low ratio will be discussed later.

**Seed destruction by bruchids and percentage of underdeveloped seeds.** The bruchid beetles found emerging from the seeds of *Prosopis chilensis* have been identified as *Rhipibruchus picturatus*, *Scutobruchus ceratioborus*, and *Scutobruchus* spp. (two undescribed species); those from *P. flexuosa* as *Rhipibruchus picturatus*, *Scutobruchus ceratioborus*, and *Scutobruchus* sp. (undescribed); and those from *P. velutina* as *Neltumius arizonensis*, *Algarobius prosopis*, and *Mimosestes amicus*.

In the 15 species of *Prosopis* surveyed (TABLE 2), averages of from 1 to 25 per cent of the seeds had been damaged by bruchids by the time of collection (shortly after fruit maturity). The variation within species was great, however, with several populations having more than 60 per cent damage. Species belonging to section STROMBOCARPA (*P. reptans*, *P. strombulifera*, and *P. torquata*) exhibited less damage than most of those in section ALGAROBIA (all other species in TABLE 2). The percentage of the seeds that were underdeveloped ranged from about 2 per cent to 53 per cent in the 83 populations surveyed, with averages for the 15 species ranging from about 7 per cent to 25 per cent.

The results obtained in the study of bruchid damage to the seeds of *Prosopis flexuosa* as a function of time are shown in TABLE 3 and FIGURE 3. By the end of the first month after fruit maturity, all the fruits had fallen to the ground, and only 2.7 per cent of the seeds had bruchid emergence holes. When the study was terminated at the end of 15 weeks, fruits could still be found beneath seven of the original nine trees, and 26.1 per cent of the seeds had bruchid emergence holes. During the first five weeks of the study, the percentage of seeds with bruchid holes remained relatively constant, but starting in the sixth week, the percentage of seeds damaged climbed at an approximately linear rate (FIGURE 3). The equation  $Y = 2.13 T - 9.56$ , obtained through linear regression analysis ( $r = 0.94$ ), estimates the amount of seed damage at any time between the fifth and fifteenth week following fruit maturity (with  $Y$  equal to the percentage of seeds with bruchid holes and  $T$  equal to the number of weeks since the first fruits reached maturity). Extreme variation is evident among the nine trees studied (FIGURE 3). Trees no. 3 and no. 4 form a striking example, growing less than 50 meters apart and suffering 0.7 per cent and 53.5 per cent seed damage respectively at the end of 15 weeks. Because the seeds of tree no. 3 were a bit smaller than average, we considered the possibility that they might not have been viable, but a test yielded 56 per cent germination, a rate that is consistent with the results of other germination tests with *P. flexuosa* (see TABLE 4 and the next section).



TABLE 2. Number of seeds per fruit, bruchid-damaged seeds, and underdeveloped seeds in species of *Prosopis*.

| SPECIES                                 | NO. OF<br>POPUL. | NO. OF<br>TREES | NO. OF<br>FRUITS | NO. OF SEEDS/<br>FRUIT | % GOOD<br>SEEDS | % BRUCHID-<br>DAMAGED<br>SEEDS | % UNDERDE-<br>VELOPED<br>SEEDS |
|---|------------------|-----------------|------------------|------------------------|-----------------|--------------------------------|--------------------------------|
| Section ALGAROBIA<br>(South America)    |                  |                 |                  |                        |                 |                                |                                |
| <i>P. alba</i>                          | 17               | 22              | 213              | 17.9±1.5               | 70.3±5.6        | 16.9±4.7                       | 13.6±2.7                       |
| <i>P. caldenia</i>                      | 4                | 47              | 377              | 19.2±0.9               | 62.3±5.7        | 15.9±3.1                       | 22.7±3.9                       |
| <i>P. chilensis</i>                     | 6                | 29              | 340              | 18.9±2.3               | 72.7±4.5        | 13.4±3.7                       | 14.0±4.3                       |
| <i>P. flexuosa</i>                      | 4                | 12              | 146              | 11.5±1.5               | 73.9±7.4        | 10.2±6.0                       | 15.0±5.4                       |
| <i>P. kuntzei</i>                       | 8                | 9               | 85               | 9.4±1.7                | 61.2±8.2        | 24.2±7.1                       | 14.6±2.0                       |
| <i>P. nigra</i>                         | 10               | 10              | 126              |                        |                 |                                |                                |
| <i>P. pugionata</i>                     | 1                | 3               | 24               | 12.2±0.6               | 91.6±0.8        | 1.5±0.1                        | 7.1±0.7                        |
| <i>P. ruscifolia</i>                    | 11               | 62              | 600              | 13.5±1.1               | 71.6±5.7        | 11.3±2.0                       | 12.8±4.2                       |
| <i>P. sericantha</i>                    | 3                | 15              | 196              | 8.0±0.7                | 76.8±4.5        | 2.8±1.5                        | 20.4±5.2                       |
| Section ALGAROBIA<br>(North America)    |                  |                 |                  |                        |                 |                                |                                |
| <i>P. glandulosa</i>                    | 3                | 7               | 57               |                        |                 |                                |                                |
| <i>P. laevigata</i>                     | 5                | 16              | 55               | 14.8±0.7               | 63.0±4.5        | 18.9±3.8                       | 17.7±2.4                       |
| <i>P. velutina</i>                      | 6                | 6               | 60               |                        |                 |                                |                                |
| Section STROMBOCARPA<br>(South America) |                  |                 |                  |                        |                 |                                |                                |
| <i>P. reptans</i>                       | 1                | 6               | 35               | 3.2±0.3                | 73.5±4.1        | 1.7±0.7                        | 24.8±4.2                       |
| <i>P. strombulifera</i>                 | 1                | 17              | 124              | 6.3±0.4                | 66.8±1.8        | 8.5±1.0                        | 24.9±1.6                       |
| <i>P. torquata</i>                      | 3                | 12              | 144              | 9.3±0.4                | 80.2±6.1        | 1.2±0.4                        | 18.6±5.7                       |



TABLE 3. Bruchid damage to seeds of *P. flexuosa*.

| TREE #    | 1    |     | 2   |      | 3   |     | 4   |      | 5   |      | 6   |      | 7   |      | 8   |      | 9   |      | TOTAL |      |
|-----------|------|-----|-----|------|-----|-----|-----|------|-----|------|-----|------|-----|------|-----|------|-----|------|-------|------|
| DATE      | no.* | %   | no. | %    | no. | %   | no. | %    | no. | %    | no. | %    | no. | %    | no. | %    | no. | %    | no.   | %    |
| ON GROUND |      |     |     |      |     |     |     |      |     |      |     |      |     |      |     |      |     |      |       |      |
| JAN. 1    | 0    | 0   | 13  | 7.9  | 0   | 0   | 8   | 5.7  | 0   | 0    | 0   | 0    | 0   | 0    | 2   | 1.8  | 2   | 1.6  | 25    | 2.1  |
| 8         | 0    | 0   | 8   | 5.6  | 1   | 0.7 | 6   | 3.4  | 8   | 5.7  | 3   | 2.0  | 1   | 0.7  | 13  | 10.7 | 6   | 4.4  | 46    | 3.1  |
| 18        | 2    | 1.6 | 1   | 0.7  | 0   | 0   | 4   | 2.3  | 4   | 3.3  | 3   | 1.9  | 4   | 2.5  | 10  | 7.11 | 8   | 4.7  | 36    | 2.7  |
| 25        | 0    | 0   | 3   | 2.3  | 0   | 0   | 4   | 2.3  | 3   | 2.5  | 8   | 4.8  | 3   | 2.2  | 6   | 3.3  | 4   | 2.5  | 31    | 2.3  |
| FEB. 1    | 1    | 0.8 | 4   | 3.3  | 1   | 0.7 | 7   | 3.9  | 6   | 5.6  | 6   | 3.8  | 0   | 0    | 7   | 5.0  | 3   | 1.7  | 35    | 2.7  |
| 8         | 1    | 0.8 | 5   | 3.4  | 0   | 0   | 18  | 11.0 | 2   | 1.7  | 3   | 1.9  | 8   | 6.5  | 2   | 1.5  | 10  | 7.6  | 49    | 3.9  |
| 18        | 2    | 1.6 | 8   | 6.3  | 0   | 0   | 30  | 20.4 | 17  | 11.3 | 9   | 5.2  | 4   | 2.9  | 19  | 13.9 | 31  | 19.7 | 120   | 9.1  |
| 25        | 3    | 2.8 | 19  | 12.8 | 0   | 0   | 12  | 9.4  | —   | —    | 10  | 6.1  | 7   | 4.5  | 6   | 6.0  | 15  | 10.9 | 72    | 6.6  |
| MAR. 1    | 0    | 0   | 33  | 25.6 | 0   | 0   | 34  | 29.1 | —   | —    | 10  | 6.5  | 10  | 6.6  | 6   | 4.9  | 11  | 8.9  | 104   | 9.7  |
| 15        | 3    | 2.9 | 40  | 31.0 | 0   | 0   | 49  | 39.6 | —   | —    | 5   | 3.3  | 2   | 1.6  | —   | —    | 19  | 12.8 | 128   | 13.1 |
| 22        | 1    | 0.8 | 17  | 12.0 | 0   | 0   | 50  | 37.3 | —   | —    | 8   | 5.1  | 1   | 0.8  | —   | —    | 22  | 18.3 | 99    | 10.4 |
| APR. 2    | 3    | 2.9 | 35  | 30.4 | 2   | 1.4 | 68  | 46.6 | —   | —    | 37  | 21.6 | 20  | 14.2 | —   | —    | 66  | 46.5 | 231   | 24.0 |
| 6         | 0    | 0   | 17  | 12.7 | 1   | 0.7 | 88  | 57.1 | —   | —    | 11  | 6.7  | 58  | 43.0 | —   | —    | 61  | 36.3 | 236   | 23.5 |
| 15        | 0    | 0   | 53  | 39.6 | 1   | 0.7 | 83  | 53.5 | —   | —    | 38  | 18.8 | 27  | 21.1 | —   | —    | 61  | 39.6 | 263   | 26.1 |
| IN TREES  |      |     |     |      |     |     |     |      |     |      |     |      |     |      |     |      |     |      |       |      |
| JAN. 1    | 0    | 0   | 1   | 0.7  | 0   | 0   | 2   | 1.0  | 2   | 1.4  | 0   | 0    | 0   | 0    | 6   | 3.1  | 1   | 0.6  | 12    | 0.8  |
| 8         | 0    | 0   | 0   | 0    | 0   | 0   | 1   | 0.6  | 0   | 0    | 0   | 0    | 0   | 0    | 0   | 0    | 0   | 0    | 1     | 0.1  |
| 18        | 0    | 0   | 3   | 2.4  | 1   | 0.8 | —   | —    | 1   | 0.8  | 3   | 1.8  | 0   | 0    | 7   | 3.9  | 5   | 2.8  | 20    | 1.7  |
| 25        | 4    | 2.6 | 0   | 0    | 0   | 0   | —   | —    | 6   | 4.8  | 6   | 3.7  | 5   | 3.0  | 9   | 4.6  | 1   | 0.6  | 31    | 2.6  |
| FEB. 1    | —    | —   | —   | —    | —   | —   | —   | —    | —   | —    | —   | —    | —   | —    | —   | —    | 5   | 3.0  | 5     | 3.0  |

\* Number of seeds with bruchid emergence holes.



It is conceivable that the seeds were too small to support the full development of a bruchid; however, tree no. 1, with average-sized seeds, also suffered virtually no bruchid damage.

All of the above data concerning seed damage (including TABLE 3 and FIGURE 3) are based on the observation of bruchid emergence holes on the outer surface of the pods. It should be noted that the actual damage at a given time is always greater than that implied by the number of emergence holes. There is no way to determine by simple observation the number of seeds that contain partially developed bruchids. FIGURE 4 presents graphically the relationship between apparent seed damage (i.e. the percentage of seeds with emergence holes) and actual seed damage (i.e. the percentage of seeds with emergence holes plus the percentage of seeds containing developing bruchids). The graph is based on data supplied to us by Ing. Agr. Arturo Terán, who tabulated the bruchid emergences subsequent to the collection date from the weekly samples of pods collected beneath eight of our study trees of *Prosopis flexuosa* and *P. chilensis*. (However, only the data from the four trees of *P. flexuosa* were used in the preparation of FIGURE 4, involving approximately 500 pods and 7000 seeds.)

Because of several unexpected problems in the field, we do not have sufficient data to describe seed damage as a function of time for *Prosopis chilensis* and *P. velutina*. In the case of *P. chilensis*, the fruits rapidly disappeared from beneath the trees, mostly having been eaten by goats; at the end of 13 weeks, we found fruits under only two of the 13 trees involved in the study, and 90 per cent of the seeds in these remaining fruits had bruchid holes. Thus from the limited data that we have, it appears that seed destruction proceeds at a much faster rate in *P. chilensis* than in *P. flexuosa*. *Prosopis velutina* was sampled only once, about one month after maturation of the first fruits in the population, and 11.5 per cent of the seeds were found to have bruchid holes. Glendening and Paulsen (1955) studied the bruchid damage to seeds of *P. velutina* over a 400-day period following fruit maturity. Their data indicate a linear increase in bruchid damage between the fifth and tenth weeks, during which time the percentage of seeds showing bruchid emergence holes climbed from about 10 per cent to about 50 per cent. After the tenth week, there was a gradual decrease in the rate of appearance of new emergence holes, so that the overall curve of damage versus time is sigmoid. Thus *P. velutina* appears to suffer a more rapid rate of damage than *P. flexuosa*, but a slower rate than *P. chilensis*.

**Germination.** The seeds of section ALGAROBIA of the genus *Prosopis*, to which the species under study belong, weigh 20–40 mg. and have the approximate dimensions  $5.5 \times 3.5 \times 2.0$  mm. (Palacios & Bravo, 1974). The leathery endocarp that surrounds each seed is impermeable to water and must be broken for the seed to germinate; repeated attempts to germinate seeds with intact endocarps yielded less than one per cent germination.



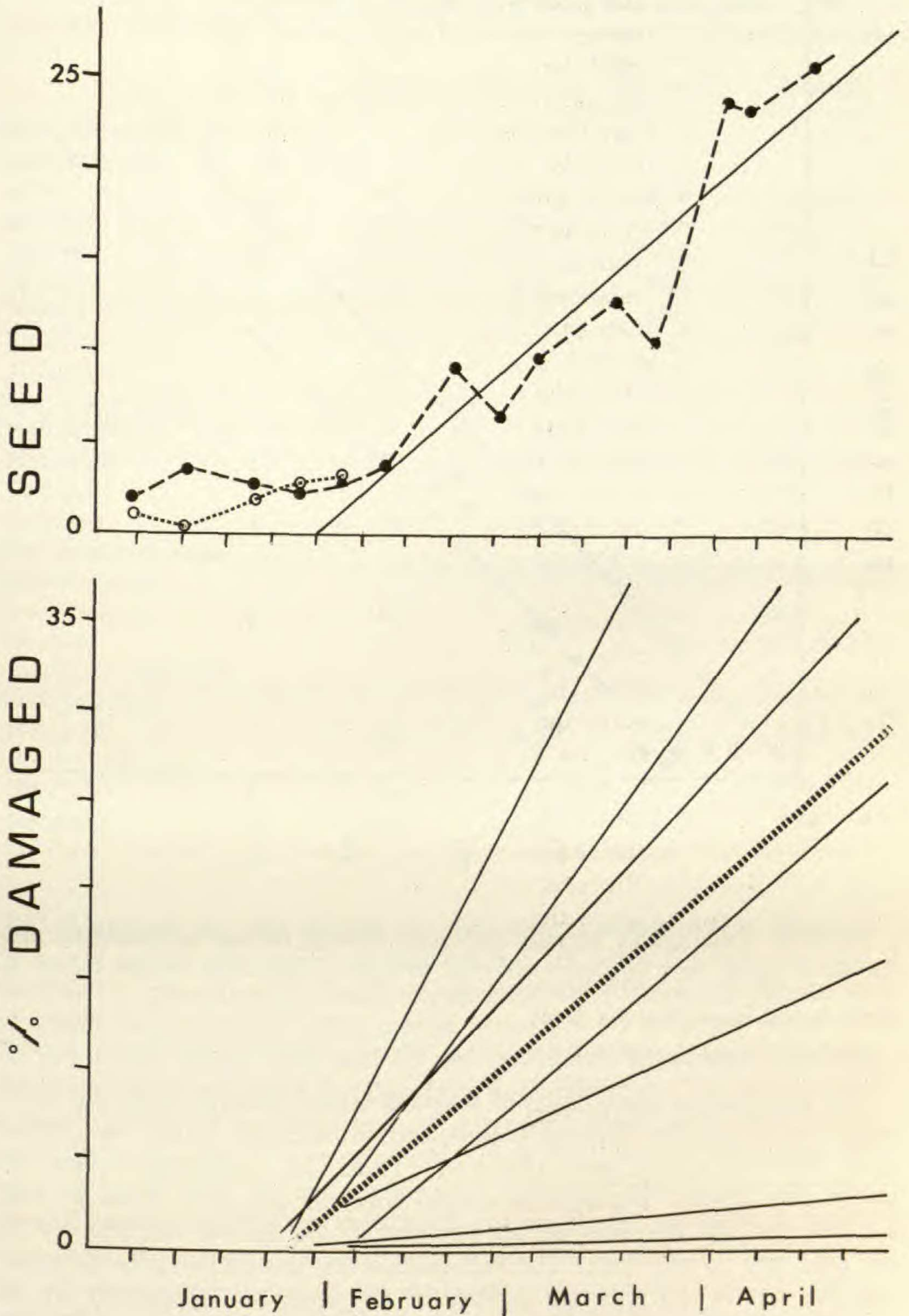


FIGURE 3. Percentage of damaged seeds in relation to time in *Prosopis flexuosa*. UPPER GRAPH: all trees together (dotted line, samples from the tree; dashed line, samples from the ground; solid line indicates regression of damage in time after 5th week ( $r=0.95$ )). LOWER GRAPH: regressions for the logarithmic phase of seed damage for individual trees ( $r$  varies from 0.96 to 0.50); note the great variation between individual trees. Broken line represents average for all trees.



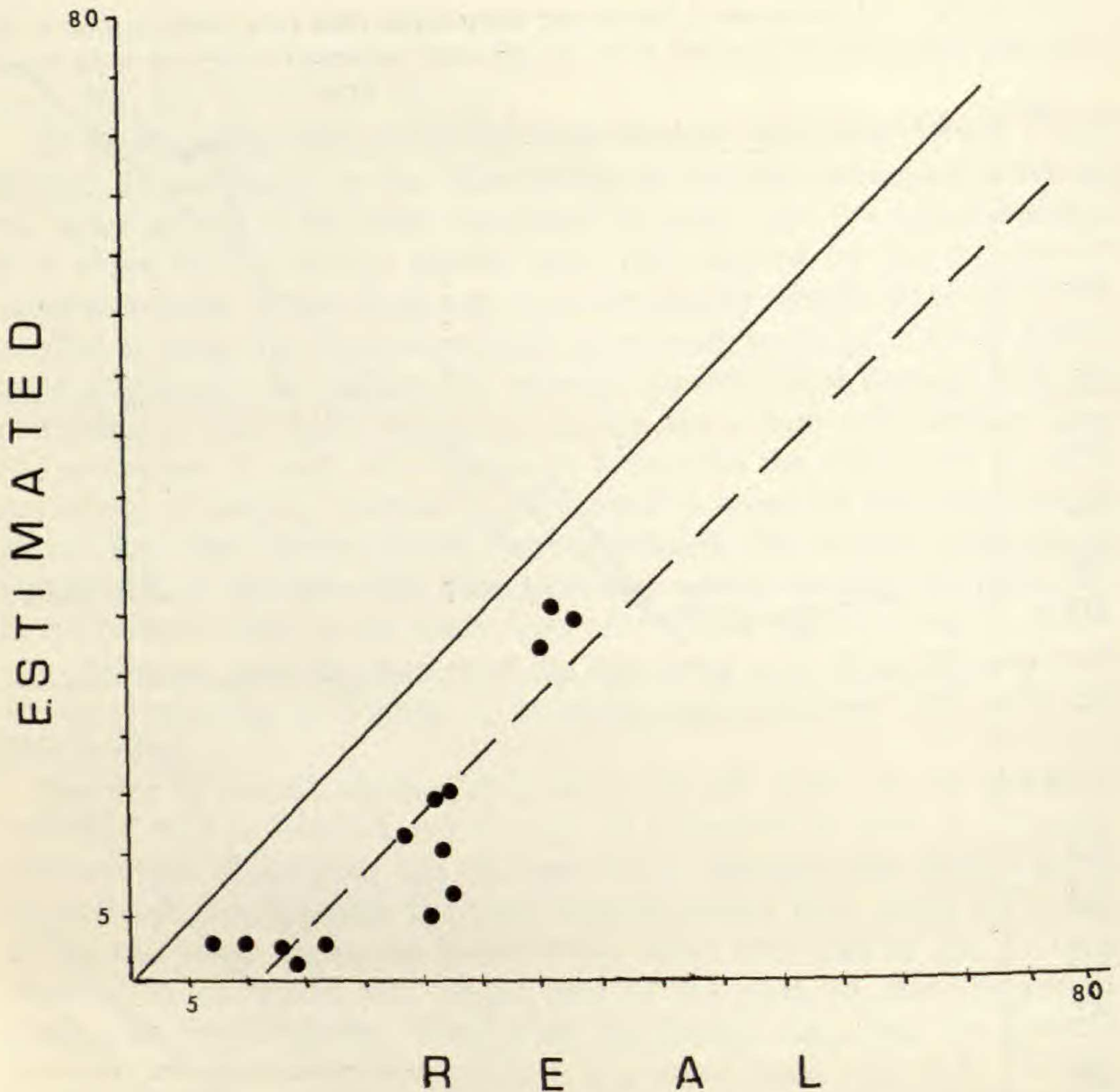


FIGURE 4. Relationship between estimated bruchid damage as shown by percentage of seeds with exit holes and real damage as indicated by percentage of seeds actually destroyed. Solid line indicates ideal 1:1 relationship; dashed line shows actual regression ( $r=0.89$ ).

The germination percentages of scarified seeds, removed from the endocarps, varied greatly between populations, to such an extent that differences between species were obscured (TABLE 4). Although values obtained for different populations ranged from 87 per cent down to only 2.5 per cent, the averages for all but four of the species fell between 25 per cent and 55 per cent. The explanation for this rather poor germination lies not in any inherent quality of the seed, but apparently in the maintenance of too low a soil temperature during the experiment. Scifres and Brock (1970a), working with *Prosopis glandulosa*, obtained up to 96 per cent germination on wet filter paper and 90 per cent in wet sand. They found the temperature of the germination medium to be a critical factor; in moist sand at 85° F., 90 per cent of the seeds had germinated after 72 hours, but in the same time period only 30 per cent germinated



TABLE 4. Germination percentages for seeds of *Prosopis* species.

| SPECIES                                 | No. OF<br>POPUL. | No. OF<br>SEEDS | GERMINATION |         |           |
|---|------------------|-----------------|-------------|---------|-----------|
|   |                  |                 | MAXIMUM     | MINIMUM | AVERAGE   |
| Section ALGAROBIA<br>(South America)    |                  |                 |             |         |           |
| <i>P. alba</i>                          | 2                | 160             | 48.8        | 10.0    | 29.4±19.4 |
| <i>P. caldenia</i>                      | 2                | 1120            | 36.2        | 16.5    | 26.4± 9.8 |
| <i>P. chilensis</i>                     | 9                | 2301            | 87.5        | 2.5     | 41.3± 6.3 |
| <i>P. flexuosa</i>                      | 3                | 263             | 74.3        | 45.0    | 54.6± 7.9 |
| <i>P. nigra</i>                         | 3                | 344             | 80.2        | 34.6    | 50.9±14.7 |
| <i>P. ruscifolia</i>                    | 1                | 160             | —           | —       | 10.7      |
| <i>P. sericantha</i>                    | 2                | 696             | 81.3        | 21.4    | 53.7± 7.4 |
| Section ALGAROBIA<br>(North America)    |                  |                 |             |         |           |
| <i>P. glandulosa</i>                    | 3                | 250             | 82.2        | 26.3    | 49.3±16.0 |
| <i>P. laevigata</i>                     | 1                | 78              | —           | —       | 29.5      |
| <i>P. velutina</i>                      | 1                | 90              | —           | —       | 82.2      |
| Section STROMBOCARPA<br>(South America) |                  |                 |             |         |           |
| <i>P. strombulifera</i>                 | 11               | 118             | —           | —       | 31.0      |
| <i>P. torquata</i>                      | 3                | 817             | 54.0        | 14.6    | 32.4±11.5 |
| Section STROMBOCARPA<br>(North America) |                  |                 |             |         |           |
| <i>P. pubescens</i>                     | 2                | 160             | 8.8         | 2.5     | 5.7± 3.2  |
| Section CAVENICARPA                     |                  |                 |             |         |           |
| <i>P. ferox</i>                         | 1                | 96              | —           | —       | 29.2      |
| <i>P. tamarugo</i>                      | 6                | 480             | 17.5        | 2.5     | 7.3± 2.2  |

at 70° F. and 42 per cent at 100° F. Similarly, Eilberg (1973) obtained 96 per cent germination with scarified seeds of *P. ruscifolia* at a temperature of 79° F. On the other hand, Glendening and Paulsen (1955), under field conditions, obtained values similar to ours.

In two trials, 20 per cent and 52 per cent germination were obtained with seeds of *Prosopis chilensis* taken from goat excrement; the corresponding trials yielded 24 per cent and 28 per cent success with seeds taken from horse excrement, 40 per cent and 12 per cent success with seeds removed by hand from the endocarps, and 2 per cent and 6 per cent success with seeds retaining the endocarps. Although the variation is great, germination percentages obtained with seeds from goat and horse excrement are comparable to values for seeds removed by hand from the endocarps, and significantly greater than values for seeds with endocarps intact.

It is worth mentioning that some of the seeds taken from excrement of goats and horses contained developing bruchids, as evidenced by the emergence of a number of adult bruchids from seeds stored inside closed containers several weeks after removal from the excrement. This contrasts with Janzen's observations concerning *Acacia cornigera*, another legumi-



nous tree which suffers seed damage from bruchid beetles; Janzen has observed that dispersal of the seeds by birds and mammals probably does not lead to bruchid dispersal because bruchid-occupied seeds are broken up as they pass through the animal (Janzen, 1969).

**Seedling development.** The seedlings of all species of *Prosopis* studied are similar in morphology, but they vary in size. They possess two fleshy, oval cotyledons averaging 2 cm. in length. The shoot shows strong apical dominance, no branching having been observed on any seedling during the two-year duration of the experiment (except in cases of damage to the apical meristem). In all species the first two to five leaves produced by the seedlings are pinnatifid, with six to ten pairs of oval leaflets, while all later leaves are bipinnatifid. Spines were often present on the first and succeeding nodes, but there was considerable variation within species, with some individuals developing no spines at all. The root is a taproot, with no obvious lateral branching. Under the favorable conditions of the greenhouse, shoot and taproot growth was rapid (TABLE 5).

## DISCUSSION

In order that the descriptive and quantitative data presented above may be of more general use, we will discuss it in the context of a theoretical model of plant population dynamics. In the process we hope to elucidate certain aspects of the reproductive "strategy" of arborescent *Prosopis* and of desert phreatophytes in general.

In a model developed by Harper and White (1971), biomass and number of individuals in plant populations are regulated by the dynamics of four successive stages of the plant's life cycle: (1) the size of the "seed bank" of viable seeds in and on the soil, (2) the "environmental sieve" that determines whether or not a seed is recruited into a population of seedlings, (3) the correlated changes in plant number and size as a seedling population becomes thinned and individuals increase in size, and (4) the phase of seed production which contributes to a new seed-rain. In our discussion we will start, for convenience, with Stage 4.

**Seed production.** The size of the seed-rain of any plant is dependent on the number of functional flowers produced, the number of ovules per flower, the efficiency of pollination (both in terms of percentage of flowers pollinated and percentage of ovules fertilized within each flower), and the mortality rate of fruits during the process of maturation due to predation and stress from the physical environment.

In *Prosopis* a huge crop of flowers is produced (in the order of several million flowers on an average tree during a single season), but only two or three flowers in a thousand initiate development into fruits. Is it reasonable to attribute this extremely low fruit/flower ratio to inefficient pollination? To attempt to answer this question, we must know something about the breeding system of the plant and the pollination agents. The



TABLE 5. Shoot growth rate in *Prosopis* (in cm.).

| SPECIES   | PLANTING<br>DATE | AGE † | 1ST MEASUREMENT |           |      |      | 2ND MEASUREMENT |    |           |      |      |
|---|------------------|-------|-----------------|-----------|------|------|-----------------|----|-----------|------|------|
|   |                  |       | N               | $\bar{x}$ | MAX. | MIN. | AGE †           | N  | $\bar{x}$ | MAX. | MIN. |
| <i>P. FLEXUOSA</i>                                  |                  |       |                 |           |      |      |                 |    |           |      |      |
| <i>Solbrig 4217</i><br>(Catamarca,<br>Andalgalá)    | 3-25             | 1     | 10              | 9.5       | 12.2 | 7.5  | 7               | 3  | 70.1      | 76   | 61   |
| <i>Solbrig 4219</i><br>(Catamarca,<br>Andalgalá)    | 3-25             | 1     | 20              | 11.9      | 14.2 | 10.3 | 7               | 6  | 70.0      | 96   | 55   |
| <i>P. CHILENSIS</i>                                 |                  |       |                 |           |      |      |                 |    |           |      |      |
| <i>Vuilleumier 1022</i><br>(La Rioja,<br>Aimogasta) | 3-13             | 1     | 76              | 13.6      | 21.5 | 4.0  | 11              | 10 | 92.2      | 117  | 62   |
| <i>Vuilleumier 1020</i><br>(La Rioja, Bazan)        | 10-22            | 2     | 42              | 8.5       | 16.8 | 2.3  | —               | —  | —         | —    | —    |

\* Growth rates of two species were studied under greenhouse conditions.

† Age in months.



flowers of *Prosopis* are protogynous. The stigma has a central depression into which the pollen must fall for fertilization to occur. Tests with *Prosopis torquata* indicate that the plants are self-incompatible (B. Simpson, personal communication). Although all three of these factors tend to reduce the efficiency of pollination (that is, the number of fertilizations per insect visitor), the following evidence indicates to us that inefficient pollination cannot be the sole explanation for the low fruit/flower ratio. The flowers are visited by many species of insects, and in such large quantities that visitors to a tree in full bloom can be heard for some distance. Furthermore, *Prosopis* trees usually grow sufficiently close together to permit cross-pollination on a large scale. Pollination efficiency is quite high within the few flowers that do produce fruit, with 50 to 100 per cent of the ovules developing into seeds. With a density of 30 to 50 flowers per cm. of inflorescence, it is highly unlikely that a bee, or other insect, would consistently pollinate a single flower only without dropping some pollen on its neighbors. By means of artificial pollination, Dr. Beryl Simpson has increased fruit production of *P. torquata* by a factor of two to four (personal communication), indicating that poor pollination is a factor contributing to a reduced fruit yield in that species. Yet even under a regime of artificially increased pollination, the fruit/flower ratio is still extremely low.

In our opinion, the production of a large number of flowers in *Prosopis* is an adaptation that serves to attract insects to the individually small (3–6 mm.) and inconspicuous flowers. In other words, the vast majority of the flowers serve as the functional equivalents of petals, although any one of them is apparently potentially capable of developing into a fruit.

The production of a great many flowers for each mature fruit is characteristic of many genera of the subfamily Mimosoideae and may well be an adaptation for insect attraction in these cases as well. A further elaboration of this theme can be found in a few Mimosoid genera, such as *Dichrostachys* and *Neptunia*, that produce dense, spicate inflorescences in which there is a floral dimorphism; showy sterile flowers are located below the less conspicuous fertile flowers, presumably attracting insects to the latter. The analogy between the sterile flowers of these genera and petals is even more apt than in the case of *Prosopis*.

Although there is no floral dimorphism in *Prosopis*, it is possible that some, or even most of the flowers are indeed sterile. Detailed anatomical studies of *Albizia lebbek*, another member of the Mimosoideae with a high flower/fruit ratio, have revealed that the embryo sacs and pollen of most of the flowers degenerate before fertilization can occur (Maheshwari, 1931). There is no obvious superficial difference between the sterile and fertile flowers in *A. lebbek*, nor is there any regularity in their relative locations on the inflorescence. Although we do not have direct evidence that degeneration of this sort occurs in *Prosopis*, it is one possible explanation for the puzzling low fruit/flower ratio. A second explanation might be the production of a chemical inhibitor in conjunction with fertilization, which in some way prevents fertilization of neighboring flowers.



In the case of either mechanism, the result would be the same; a great quantity of flowers could be produced, attracting insects and ensuring pollination, while limiting the fruit initiations to the small number that the plant could support.

As can be seen in TABLES 1 and 2, there is considerable variation between individuals and populations in the number of fruits produced per thousand flowers and the number of fully developed seeds per fruit. Many factors, both genetic and environmental, may be contributing to this variation, but we do not have sufficient data to determine its cause with any certainty. In spite of the variation, however, we can make a rough estimate of the quantity of seeds produced by an average tree in one reproductive season. We have already stated that an average tree of *Prosopis chilensis* produces several million flowers (we will use 10 million as a very rough estimate) and that one mature fruit is produced for every 10,000 flowers. An average fruit contains 19 seeds (see TABLE 2). Multiplying the three factors yields a result of 19,000 seeds/tree/reproductive season. By the same method, we have calculated that an average tree of *P. flexuosa* produces about 80,000 seeds. An actual count of the total seed crop of a tree of *P. velutina* by Glendening and Paulsen (1955) yielded 142,000 seeds. Combining these estimates and taking into account a large margin of error for our gross approximation of the number of flowers on a tree, we can state that on the order of  $10^4$  to  $10^5$  seeds are produced by a *Prosopis* tree in a single reproductive season.

**The seed-bank.** Shortly after a fruit reaches maturity, an abscission layer forms at the base of the pedicel and the fruit falls to the ground; there its complement of seeds become components of the "seed-bank," subject to the action of the "environmental sieve." Little is known about the size of the seed-bank of arborescent *Prosopis*. Seeds of *P. velutina* have been found to be viable after 50 years storage in a herbarium (Glendening & Paulsen, 1955), and it has been shown that they may remain viable in the soil for at least 10 years (Tschirley & Martin, 1960). However, Glendening and Paulsen found that seeds of *P. velutina* deteriorated considerably during two years of storage in soil and that none germinated under field conditions after three years. How many viable seeds actually exist in the soil in any given area is unknown.

**The environmental sieve.** The "environmental sieve," as defined by Harper and White (1971), is the sum of environmental factors which determine whether or not a particular seed will be recruited into the seedling population. The sieve can be viewed as comprising three components: the physical environment, the biological environment, and dispersal. Two of the components, the physical environment of the soil and the biological environment (attack by herbivores and microorganisms), act upon the seed once it has come to rest. The third component, dispersal, determines where the seed will come to rest and thus influences which set of physical and biological factors will act upon the seed. The biological component of



the sieve, being the first to exert a strong effect on the population of newly produced *Prosopis* seeds, will be discussed first.

As far as we have been able to determine, the only herbivores that effect a significant reduction in the population of freshly produced seeds are the bruchid beetles. The adult bruchid lays its eggs on the outside of the developing fruit. When the eggs hatch, the larvae burrow into the fruit, a single larva settling inside each attacked seed. After a number of weeks (the exact development time of the species that attack *Prosopis* is not known), the adults emerge from the seeds, having destroyed them in the process. In many species of bruchids, including some and possibly all of those that attack *Prosopis*, the adults may oviposit shortly after emergence from the seed, allowing a rapid succession of attacking bruchid generations.

D. H. Janzen (1969) has developed a body of theory concerning the evolutionary "strategies" by which the seeds of tropical leguminous trees escape destruction by bruchids. The underlying premise, upon which Janzen bases the existence of a selection pressure sufficiently strong to drive the evolution of seed-escape mechanisms, is that virtually all seeds of a bruchid-attacked species that remain on or beneath the tree will be destroyed by succeeding generations of bruchids. Dispersal, as Janzen points out, is therefore of great importance as a means of escape from the inevitable destruction that will occur if the seed remains near the tree.

Our data lend support to the premise of eventual destruction of virtually all nondispersed seeds, but the data are ambiguous concerning the importance of bruchid attack relative to other factors that might prevent germination beneath the parent tree. The fruits of *Prosopis chilensis* are rapidly dispersed by livestock and water, but the few fruits that remained beneath the tagged trees 13 weeks after maturity had already suffered 90 per cent seed destruction by bruchids. Several seedlings were found growing out of decaying pods beneath one tree of *P. chilensis*, indicating that at least a few seeds escape destruction by bruchids without dispersal. No second-year plants or saplings have been observed beneath tagged trees, nor have we ever seen young *Prosopis* plants directly beneath the crown of any tree. However we have, on rare occasions, observed young plants one to two meters in height within three meters of the edge of the area shaded by the crown of a tree of *P. chilensis*. There is, of course, no way of knowing whether these young plants developed from undispersed seeds of the nearby tree that escaped destruction by bruchids, or from seeds of a different tree that were carried to their present position by animals or flood waters.

The fruits of *Prosopis flexuosa* are attacked at a much slower rate, but dispersal is also slower. At the termination of the study, 15 weeks after fruit maturity, only 26 per cent of the seeds had bruchid emergence holes, but there were still large quantities of fruits lying beneath a number of the tagged trees. Assuming a continuation of the linear rate of seed destruction that occurred between the fifth and fifteenth week (FIGURE 3), all the seeds would theoretically be destroyed by the 51st week after fruit



maturity. However, in actuality, the fruits disappear from beneath the trees well before the 51 weeks have passed. (We found no fruits beneath the trees in November, approximately 40 weeks after the maturation of the previous year's crop.) We can make no estimate concerning the final percentage of nondispersed seeds of *P. flexuosa* that are actually destroyed by bruchids; however, we observed no seedlings or saplings beneath or near any tree of that species. We can conclude, then, from our data on both species, that owing to bruchid attack and possibly other factors (e.g., insufficient sunlight beneath the parent tree), dispersal is almost a prerequisite for seedling establishment.

The slower rate of attack on *Prosopis flexuosa* fruits and the apparent immunity of certain trees of that species to attack by bruchids raises the possibility that *P. flexuosa* may have evolved a chemical defense against bruchids. We lack direct evidence, but it is known (Carman, 1973) that the foliage of *Prosopis* contains toxic nonproteinaceous amino acids. Therefore, it is quite conceivable that a compound toxic to bruchids might be present in the seeds. There are, however, other possible explanations for the low rate of seed destruction in *P. flexuosa*, and we are not presently in a position to judge which is correct.

The importance of dispersal as a means of escape from the parent tree has been pointed out. It should also be noted that the earlier the dispersal occurs, the less likely will be the destruction of any given seed by bruchids. As Janzen (1969) has observed, the strong selection pressure created by bruchid attack has led to the evolution in the Leguminosae of mechanisms that facilitate rapid seed dispersal; the fruit of *Prosopis* is apparently such an adaptation. The mature fruit consists of a single-layered exocarp, a multilayered mesocarp, and a tough, leathery endocarp that surrounds each seed individually. The mesocarp is fleshy, sweet, and nutritious; Catlin (1925) found it to have a protein content of 13.91 per cent. Many kinds of mammals eat the fruits and eject the seeds, undamaged, in their feces. The present dispersal agents are predominantly domesticated ungulates (goats and horses in Argentina; cattle and horses in Arizona), which are extremely efficient in fruit removal. In the parts of the Argentine study site where goats were present, they removed all fruits from beneath tagged *P. chilensis* trees within two weeks after fruit-drop. Similarly, cattle removed all fruits from beneath tagged *P. velutina* trees within two weeks after fruit-drop. The marked trees of *P. flexuosa*, on the other hand, were located in an area where no livestock ranged, a fact that is largely responsible for the much slower dispersal of the fruits of that species. Among wild native mammals, foxes, armadillos, skunks, jack rabbits, cottontail rabbits, coyotes, wolves, and assorted small rodents, particularly kangaroo rats and woodrats, are known to eat the fruits (Graham, 1941; Martin, *et al.*, 1951; D. Greigor, personal communication), but their combined effect on dispersal is today probably of relatively little consequence in comparison to the magnitude and rapidity of dispersal by livestock.

It is well known that the seeds of a number of species of *Prosopis* are



able to germinate after passage through the digestive tract of mammalian dispersal agents, as demonstrated by the presence of seedlings growing out of the excrement of horses and cattle. This has been documented by the work of Glendening and Paulsen (1955) on *P. velutina*, the work of Eilberg (1973) on *P. ruscifolia*, and our germination tests with seeds of *P. chilensis* taken from the excrement of goats and horses. While the endocarps are usually removed from the seeds during passage through the digestive tract of goats and cattle, it was observed that many of the seeds found in the feces of horses and foxes retained their endocarps. The endocarps in horse excrement were generally cracked and thus no longer able to impede germination, but the endocarps usually emerged unbroken in the feces of foxes. Thus the seeds dispersed by foxes must await the additional process of breakage of the endocarp before germination can occur, whereas the seeds dispersed by goats, cattle, and horses can germinate soon after excretion, if the environmental conditions permit.

Although mammals are the most important dispersal agents, water clearly contributes to the process, and birds and ants may play a part as well. The fruits of *Prosopis chilensis* and *P. velutina*, species that grow along washes, are subject to dispersal by water during summer flash floods. Fruits that have dropped to the river bed from overhanging branches are swept away and probably broken up by the crushing action of boulders in the churning waters. Although some seeds may be destroyed in the process, it is likely that many survive to be deposited in the river bed or on its banks when the waters subside. In the austral summer of 1973, a particularly wet season, floods were an important source of fruit dispersal for *P. chilensis* trees growing in areas where there were no goats. *Prosopis flexuosa* can occur along washes, but most of the trees of this species in the Argentine study area grow on the interfluvial flats where water-dispersal of this kind cannot occur. (We did observe one case in which the fruits of a *P. flexuosa* tree on the flats were swept away by overland sheet flow after a particularly heavy rainstorm, but this was unusual.) The lack of water-dispersal and the absence of livestock in the *P. flexuosa* study sites are, together, quite sufficient to explain the slow rate of dispersal of this species in comparison with that of *P. chilensis*.

Birds probably play little part in the dispersal of *Prosopis* seeds at the Argentine site but may be more important in Arizona. The only birds that we have observed eating *Prosopis* fruits in Argentina are parrots, which generally attack the fruits while they are still on the tree, eating the fleshy mesocarp and letting the seeds fall to the ground still enclosed in the tough endocarps. The seeds dropped by the parrots may escape attack by bruchids (it is not known whether the adult beetles will lay eggs on a naked endocarp removed from the fruit), but, as we pointed out earlier, it is highly unlikely that any seedling would survive and become established beneath the crown of the parent tree. A number of other birds that occur in the Argentine study area (*Eudromia elegans*, *Columba maculosa*, *Zenaida auriculata*, and possibly *Rhea americana*) are likely to feed on *Prosopis* fruits, but we have not actually observed any doing so.



According to Martin, *et al.* (1951), *Prosopis* seeds are eaten extensively in the southwestern United States by the gambel's quail (*Lophortyx gambelii*), and occasionally by white-winged doves, ravens, and two other species of quail. We have no observations of this occurrence ourselves and can make no comment on its significance in terms of dispersal or predation.

Ants have been observed in Argentina carrying individual *Prosopis* seeds, still enclosed in the endocarps, and even whole sections of fruits. According to Dr. Jim Hunt (personal communication), the ants involved, *Acromyrmex lobicornis* and *A. striatus*, are "gardening ants" that carry vegetable matter of all kinds into their subterranean nests, where it serves as a substrate for the specialized fungi that the ants culture and use for food. The seed, which may be carried as much as 50 meters from the tree, is not eaten by the ants, but it is uncertain whether it would remain viable after serving as a fungal substrate. At any rate, the frequency of seed-removal by ants does not appear to be great enough to be considered significant in terms of either predation or dispersal.

At the beginning of our discussion of the "environmental sieve," we stated that the importance of dispersal as a component of the sieve lies in its function as a determinant of the location where the seed will come to rest and, consequently, the set of physical and biological stresses that will be brought to bear on the seed. The various modes of dispersal should be considered, then, in terms of the precision with which they place *Prosopis* seeds in a position that is favorable for germination. Water-dispersal has the advantage that the seeds are necessarily deposited along the wash, the habitat where the mature trees grow and therefore presumably the most favorable environment for germination or subsequent survival or both. Animals and birds, on the other hand, undoubtedly excrete many seeds in places, such as exposed flats, where they have no chance of germination, although loss of seeds in this manner is somewhat reduced by the tendency on the part of many animals to stay in the washes because that is where the food is. Balanced against this advantage of flood-dispersal is the irregularity of its breaking effect on the fruits; it is probable that many seeds are crushed by rocks, while others are not freed from the endocarp or remain inside an intact portion of the fruit. In the passage through the mammalian digestive tract, on the other hand, seed survivorship is high and, in some animal species, the endocarps are broken with factory precision, preparing the seeds for quick germination. If we are correct in our premise that the fruit of *Prosopis* is specialized for dispersal by animals, not water, this in itself indicates that in the long run animal-dispersal produces more germinations in locations favorable for maturation than does water-dispersal (or, more accurately, that it did in the region where the genus evolved). It is worth mentioning, however, that at least one related species of tree (*Acacia caven*), growing in the same general habitat as *Prosopis* at the Argentine site, has fruits that are apparently adapted for water-dispersal.

Two components of the "environmental sieve" have now been discussed.



The remaining component, the suitability of the physical environment at the location where the seed comes to rest, will ultimately determine which of the relatively few surviving seeds will germinate and become established. Assuming that the endocarp has been removed or broken in the process of dispersal and the seed scarified, germination and subsequent survival of the seedling are dependent upon the depth at which the seed is located, the soil temperature, and the soil moisture.

Scifres and Brock (1970b), working with *Prosopis glandulosa*, found depth of planting to be a critical factor in seedling emergence. Under favorable temperature and moisture conditions in the laboratory, seedlings emerged from 80 per cent of the seeds planted at 0.5 to 1.0 cm., as compared to less than 20 per cent emergence from seeds planted below 2.0 cm. Interestingly, 100 per cent of the seeds placed on top of the soil germinated, but in no case did seedling establishment occur. The low probability of germination of deeply placed seeds is a factor that would probably work against seeds dispersed in a flash flood.

The importance of soil temperature has already been pointed out, 80° to 85° F. being the most favorable temperature for the species for which data are available (*Prosopis rusCIFolia*, *P. velutina*, *P. glandulosa*).

For plants of the desert environment, the amount of moisture present in the upper levels of the soil and the timing of its availability are the most critical factors influencing germination and seedling survival. We suspect that the seedlings of phreatophytes are particularly vulnerable to drought, as a consequence of the survival strategy of the mature plant. Owing to their ability to tap a constant water supply, phreatophytes have not been forced to evolve the extensive physiological and morphological adaptations that allow such drought-resistant shrubs as *Larrea cuneifolia* and *Tricomaria usillo* to survive. As a result, the phreatophyte seedling is in a particularly vulnerable position, lacking both the deep root system of the parent tree and the high degree of morphological adaptation of the seedlings of desert shrubs. Indeed, it seems amazing to us that *Prosopis* seedlings ever become established at all in the region of the Argentine study area, where the dry season usually lasts nine months or more. Judging from the scarcity of both seedlings and saplings in that area, germination is a rare event, and establishment must occur only in those very unusual years when heavy summer rains are combined with occasional light rains at intervals during the winter drought, allowing the young plant to survive the first critical year. Seedling establishment is probably considerably easier for *P. velutina* in Arizona, where there are summer and winter rainy seasons.

It would be interesting to survey the age structure of a population of *Prosopis chilensis* or *P. flexuosa*; we suspect that the result would show that most of the trees germinated during a very few years. Furthermore, if we are correct in our premise that phreatophyte seedlings are more vulnerable than the seedlings of desert-adapted shrubs, a study comparing the age structures of populations of *P. chilensis* and of a dominant shrub of the same region, such as *Larrea cuneifolia*, should show that the



shrubs became established during a greater number of years than the *Prosopis*.

For an "opportunistic" desert species that can become established only in rare wet years, the seed-longevity of 50 years that has been documented for *Prosopis velutina* is clearly an advantage; whether seeds can survive that long under field conditions is, however, doubtful (Glendening & Paulsen, 1955). Also advantageous are the rapid growth of the taproot in *Prosopis* seedlings and the timing of fruit-drop at the beginning of the summer rainy season; both factors help maximize the depth reached by the root during the brief period of optimum growth conditions, which in turn maximizes the probability of survival until the next rain. The advantageous timing of fruit-drop in *Prosopis* is made possible by its phreatophytic habit. For most desert perennials, blooming is tied to the timing of rainfall, but the availability of a constant water supply gives the phreatophyte the flexibility to bloom at whatever time is most favorable for subsequent germination of the seeds produced.

#### ACKNOWLEDGMENTS

We should like to thank Jerry LeClaire, John Cross, and Charles Lowe for their help in obtaining information on flower and seed production; John Kingsolver and Arturo Terán for identifying the bruchid beetles and allowing the use of unpublished data; Yoko Abe, Gordon Brown, Jerry LeClaire, Paul Reppun, and T. W. Yang for allowing us to use their unpublished phenological data; and Bernice Schubert and Beryl Simpson for reading the manuscript and making valuable comments. Grant GB-27150 from the the National Science Foundation (principal investigator, Otto T. Solbrig) made field research in Argentina and Arizona possible and aided us in other ways. To all we are very grateful.

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